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Plant sentience: The burden of proof

Commentary on [Segundo-Ortin & Calvo](#) on *Plant Sentience*

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Abstract: Segundo-Ortin & Calvo's (2023) target article takes a less speculative and more evidence-based approach to plant sentience than did previous works promoting that idea. However, it retains many of the idea's longstanding difficulties such as starting from a false dichotomy (plants must be either hardwired or sentient), not accepting the full burden of proof for an extraordinary claim, confusingly redefining accepted cognitive terms, implying cell consciousness, not adopting the most parsimonious explanations for plant behaviors, and downplaying all the counterevidence. We advise rectifying these problems before plant sentience can become a full-fledged scientific domain.



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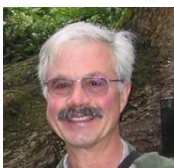


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1. Positive aspects. Although we are not proponents of the idea of “plant neurobiologists” that plants are sentient (conscious) organisms, we recognize the target article by Segundo-Ortin & Calvo (2023; henceforth S&C) as being an improvement on the previous literature on this topic. The extensive literature review, much of it previously published (S&C, 2021), will acquaint animal scientists with the remarkable sensitivity of plants to their environment—a contribution that also drew praise from several other commentators (Brooks Pribac, 2023; Gutfreund, 2023; Pessoa, 2023; Struik, 2023; Yilmaz, 2023).

S&C, having been criticized in the past for being too speculative (Mallatt et al. 2021a,b), have taken a more circumspect and evidence-based approach this time by tempering their arguments with a more critical analysis of data reported in the literature. Another good development is that they are performing their own experiments to test for associative learning in pea plants (S&C, p. 10) and for a putative form of vision in the mimic plant, *Boquila* (p. 12). Furthermore, they cite much more of the opposing literature for a more even treatment than in past publications that promoted plant sentience.

Another positive attribute is that S&C did not explicitly accept the idea of the “Cellular Basis of Consciousness” (CBC, Reber, 2016), a version of biopsychism (according to which all cells and life are conscious: Reber, 2019; Reber et al., 2022; Thompson, 2022). Aside from a lack of evidence, that idea is beset with difficulties, such as explaining how every cell in our body can be conscious when brain injury is what turns off our consciousness (Mallatt & Feinberg, 2017; Mallatt et al., 2021a). As Safina (2016) said, your body’s “other cells don’t keep your mind going when your brain is gone.” Such considerations make biopsychism counterfactual, self-contradictory, and difficult if not impossible to test scientifically.

Apart from these improvements in a scientific direction, however, S&C still face many of the original difficulties of their claim (e.g., as presented by Calvo, 2017; Calvo & Trewavas, 2020; Trewavas et al., 2020) that plants are sentient. One difficulty is that much of their case is built on arguing from analogy, an approach that is fraught with pitfalls (Struik, 2023; Robinson et al., 2023). Instead of analogies, what is required in the case of plants is rigorous and compelling evidence, because plants lack the neurons, synapses, and brains that are associated with sentience in animals (Feinberg and Mallatt, 2016; Taiz et al., 2022). Our other concerns will be presented one by one:

2. False dichotomy. Proponents of plant sentience posit a false dichotomy by acknowledging only two possible explanations of plant behavior, hence if one is wrong the other must be right. According to S&C, plant behavior is either (1) hardwired, mechanical, and inflexible (in their mischaracterization of the traditional view), or (2) sentient, volitional, cognitive, and intelligent. But there is a third, intermediate, possibility—that plant behavior is flexible and complex but does not involve sentience. To show that this option exists one example is enough: In humans, swallowing and breathing are nonconscious behaviors (in the sense that comatose people perform them) produced by central pattern generators in our brain (Panneton & Lechner, 2012; Yamamoto et al., 2022). This implementation does not make these behaviors inflexible; indeed, they are modified by different internal and external signals. For example, breathing rates are altered by a build-up of carbon dioxide in our blood or by low oxygen pressure in high altitude. In fact, all living organisms make adjustments to maintain *homeostasis* (Billman 2020), so none are hardwired in the sense of an electronic circuit. It is simply incorrect to assume that if plants are not automata, they must be sentient.

Plants have evolved the capacity to integrate multiple sensory signals and to respond accordingly (Taiz et al., 2022). For example, multiple factors can influence their flowering time, including day-length, irradiance, temperature, mineral nutrients, and more. These are

genetically programmed responses to environmental factors that provide flexibility to the plant's behavior.

Another example is the pairs of guard cells around tiny stomata (holes) in the leaf epidermis that regulate gas exchange as well as water loss from the plant. Each pair of guard cells integrates multiple signals to regulate the stomatal aperture, including light, CO₂, leaf water potential, pathogens, temperature, and the time of day (Jezek & Blatt, 2017; Blatt et al., 2022). Every square millimeter of a typical leaf contains around 200-300 stomata, each of which regulates its aperture independently. It is absurd to regard each "decision-making" pair of guard cells as an independent sentient being. Thus, plants are better understood as complex adaptive systems that are able to respond appropriately to changing environmental conditions. This adaptability is an emergent property of the plant genome that does not require sentience.

3. Burden of proof. According to the "Sagan Standard" in science, extraordinary claims must be backed up by extraordinary evidence (Sagan, 1986). S&C say they are aware that the burden of proof is on those who claim plants are sentient (p. 18), but if so, why has this group promoted plant sentience for years without first providing compelling evidence? If they accept the responsibility as their own, then why ask *other* researchers to address and explore whether plants are sentient (top of p. 2)? Why challenge the opponents to prove the null hypothesis (that plants are *not* sentient) by stating that "there is no reason to suppose that [plants] could *not* have evolved . . . sentience" (p. 19)? S&C also seem to sidestep the burden of proof by labeling their opponents "zoocentric," meaning unwilling to consider that organisms other than animals may be sentient (pp. 1-2). No, the opponents are not close-minded or myopic, but are just declining to accept, without strong evidence, the extraordinary claim that plant sentience is produced by some unknown, hypothetical mechanism that does not involve a nervous system. It is now incumbent on plant neurobiologists to accept unequivocally that the burden of proof lies squarely on their shoulders.

4. Redefined cognitive terms. Plant neurobiologists, including S&C, have redefined standard neuropsychological terms, giving them unfamiliar meanings that fit plant behaviors. Although this tendency has been pointed out before (Taiz et al., 2019, 2020; Mallatt et al., 2021c; Struik, 2023; ten Cate, 2023), S&C's target article presents all the redefinitions together; hence we can consider them here to illustrate the problems they raise.

Cognition is generally defined with respect to thinking and knowing, and as involving a brain: for example: "the mental action or process of acquiring knowledge and understanding through thought, experience, and the senses" ([Oxford Languages](#)). Yet S&C do not include the mental aspect, relating cognition only to the "manipulation of the environment in order to enable metabolic functioning" and "behavioral patterns that are adaptive, flexible, anticipatory and goal-directed" (p. 4). In his commentary, Ten Cate (2023) disagrees with S&C's definition of cognition. Although his own definition does not demand a brain or mental processes, it requires a consideration of the *causal mechanisms* behind behaviors, which S&C's definition leaves out. Instead, S&C only consider adaptive responses. Merely being adaptive is not a criterion for the presence of cognitive or sentient processes (ten Cate, 2023, pp. 2-3; see also Mallatt et al., 2021a, pp. 461-462).

Decision-making, in standard definitions, involves minds and mental pondering: "making up one's mind as to an opinion, course of action, etc." (Oxford English Dictionary). But S&C use the following redefinition of Reid et al. (2015) that does not require a mind as a central controller: "the action by an entity (individual organism or group) of selecting an

option from a set of alternatives, based on characteristics of the alternatives that the entity can perceive" (p. 7).

"Neurobiology" and **"nervous system"** are redefined as carrying out the functions of interest, such as long-distance electrical signaling, rather than as a structure; so no nervous tissue is required (pp. 3, 16, 18). (S&C's redefinition of a **"neurotransmitter"** as not needing a neuron-to-neuron synapse, nor any nervous tissue at all, was discussed in our other commentary: Robinson et al., 2023.)

Our concern about all these alternative definitions, which animal neurobiologists will reject, is that they will cause so much confusion and miscommunication that proper experimental tests of plant sentience can never be designed or executed.

5. Regression to biopsychism. Although S&C did not explicitly accept cell consciousness, most of the plant behaviors they present are also performed by one-celled organisms, including bacteria. These include communication, kin recognition, "decision-making," mimicry, etc. (Reid et al., 2015; Wall, 2016; de Groot & Torrent Burgas, 2020). Therefore, S&C implicitly accept biopsychism, which is arguably even more controversial than plant sentience.

6. Imparsimony. Assuming that sentience is a highly complex phenomenon arising from complex physical processes (Mallatt & Feinberg, 2021), we reason that if a behavior can be explained more simply by known physiological or biochemical processes, then that behavior does not rely on sentience. Simplest explanations are preferred. This is the parsimony principle that guides scientific inquiry. The proponents of plant sentience fail to apply it.

7. Behaviors that are not sentient. When our parsimony criterion is applied, most of the plant behaviors that S&C say indicate sentience do not do so. We have analyzed the behaviors from their Section 2; almost all can be explained more simply. For example, *communication*, *kin recognition*, *foraging*, *mimicry*, and *swarm intelligence* can all be explained by chemical-signal molecules or other specific cues that affect membrane receptors and thereby induce a direct response (e.g., Mastinu, 2023).

7.1 Decision-making. The ability to make decisions is the proposed indicator of plant sentience that S&C cover most thoroughly (pp. 6-8). But S&C's concept of a decision, as a choice between alternative courses of action in the face of multiple competing stimuli, does not need sentience. Instead, such an outcome could result simply from whichever sensory cue is strongest, or from the stimulus whose genetically programmed receptor molecules are most abundant, or the stimulus whose receptors are most important for survival as determined by natural selection. In the practical sense, the nonsentient "decision" could just consist of plants growing along trails of attractive molecules to reach a goal that enhances their survival (e.g., the parasitic dodder plant that follows volatile organic compounds: Runyon, 2006). Other nonsentient "decisions" could arise from growing in a direction that avoids danger signals, as in Li and Zhang's (2008) demonstration that *Arabidopsis* roots avoid salty regions of soil.

The trade-offs that S&C call decisions could be explained instead by a simple internal program that says "grow away from this negative signal" (emitted by a competitor plant) except when that program is overridden by another signal that enhances survival (e.g., grow to a nutrient patch in the soil: Cahill et al., 2010). Such simple explanations can be extended to those trade-offs that minimize a plant's risk-sensitivity (S&C, p. 8). None of these choices requires a sentient decision, as any textbook of modern control engineering

(Bissell, 2017), adaptive robotics (Billard et al, 2022), or homeostasis (Billman 2020) can illustrate.

It is unlikely that plants make true, sentient decisions because all plants in a population tend to respond to a stimulus in the same way under the same environmental conditions, whereas if they had sentient volition, some would decide to act differently. Reid et al. (2015) claim that phototropism, in which plants grow toward a source of light, is a sentient decision. However, the mechanism of phototropism is quite well understood and does not involve any kind of mental processing before bending toward the light source (Briggs & Christie, 2002; Fiorucci & Fankhauser, 2017). Except in the case of well-defined mutations that block light perception, 100% of the seedlings bend toward the light. If the plant had to decide whether or not to bend toward the light, surely some plants would decide not to bend. Because plants are genetically predisposed to bend toward light there is no need to invoke sentient decision-making in plants. To do so is to make the classic error, dating back to Aristotle, of applying teleological reasoning to a physiological phenomenon that evolved by natural selection.

7.2 Learning and memory. On the question of whether plants learn well enough to indicate they are sentient, S&C commendably reserve judgement, saying that more experimental evidence is needed (pp. 9-10). However, they devote their long, full-page discussion to presenting the sparse and inconclusive findings without ever pointing out how little evidence actually exists. Despite decades of experimental investigation, the only types of learning that have been discovered in plants are simple habituation and a few much-debated results for classical associative learning (Adelman, 2018; Gagliano et al., 2014, 2016; Markel, 2020). These learning types do not indicate sentience because the spinal cord of a live human or rat, when severed from the brain and obviously not conscious, can still learn in these ways (Grau et al., 1998; Mallatt et al., 2021a). Only an advanced type of learning, of completely novel behaviors that involve the whole body, are evidence of sentience (Feinberg & Mallatt, 2016, p. 152; Ginsburg & Jablonka, 2019; Birch et al., 2020). The criteria for learning and sentience in invertebrates (Crump et al. 2022) are far more exacting and rigorous than those S&C used for plants.

7.3 Numerosity. S&C also claim that plants have sentience-based *numerical competence* (the ability to count, pp. 12-13). The evidence they cite is that the trigger hairs on a trap of the Venus flytrap usually need to be touched *twice* for the trap to snap shut. Iosip et al. (2023) found that this requirement stems from simple physiology: two touch-induced action potentials—with their accompanying waves of Ca^{+2} travelling over the trap—are needed for enough Ca^{+2} to enter the target cells and thereby spring the trap. This is an elementary threshold effect rather than sentient counting.

7.4 Valence. S&C call for more studies on whether plants have “valenced sentience,” which is “the organism’s ability to assign a value (advantage/good vs. harm/bad) to a particular stimulus” (or set of stimuli) (Lyon et al., 2021). Valence is the basis of the affective form of sentience—of feeling emotions, moods, pain and pleasure (Feinberg & Mallatt, 2018). However, the studies that S&C cite as suggesting valence merely show that plants avoid harmful stimuli (e.g., roots grow to escape from strong light: Yokawa et al, 2013; Yan et al., 2022). Such avoidance, however, is readily explained as a physiological reflex, and reflexes are not sentient (Feinberg & Mallatt, 2016, Chapters 7-8). From an ethical perspective, one must be extremely cautious in proposing without proof that plants assign “a negative value to aversive stimuli” (S&C, p. 19) because that would imply that plants suffer when humans harvest, cut up, cook, and eat them (Brooks Pribac, 2023; Milburn, 2023; S&C). In contrast

to the complete lack of evidence that this is true of the human consumption of plants, the evidence that farmed animals have valenced sentience is overwhelming (Birch, 2017; Rowan et al., 2021).

7.5 Anticipatory behavior. S&C give two examples of what they say are sentience-based anticipatory behaviors in plants (p. 9). The first is leaves of the Cornish Mallow *Lavatera* reorienting to the east overnight to face where the sun will rise in the morning (Schwartz & Koller, 1986; Garcia Rodriguez & Calvo Garzon, 2010). The second example is roots of the pea plant *Pisum* growing into nutrient patches that are *increasing* in nutrients and not just high in nutrients in the absolute sense (Shemesh et al., 2010). In both cases, however, it seems that simple commands could be programmed into the plants' growth modules: *Lavatera* could have an inherent timer plus a command to 'reorient to the opposite direction of the previous sundown,' and *Pisum* roots could have a command to respond to increasing nutrients. No sentience would be required.

One study discussed by S&C, however, does seem to show a true anticipatory behavior through operant learning. Mittelbach et al. (2019) present evidence that flowers of the Andean plant *Nasa poissoniana* anticipate revisits of (simulated) pollinators by learning from the intervals between the pollinators' previous visits. That is, the flowers learn to delay swinging their stamens toward their center after they have been trained on the time when a pollinator will arrive there. Statistical tests firmly support their conclusion (their Fig. 1), although the large variation between the responses of different plants raises some questions (see their Fig. S3). Another caveat is that the experiments used an artificial stimulus to initiate the response: a needle that bent the nectar-scale trigger rather than an insect (e.g., carpenter bee) as in nature. These considerations suggest that the experiments need to be replicated and extended. Moreover, although *Nasa* flowers may indeed have anticipatory learning, such learning is thought to indicate sentience only when it involves the whole body rather than just one organ/flower ('global operant responses' of Feinberg & Mallatt, 2016, p. 152; and 'unlimited associative learning' of Ginsburg & Jablonka, 2019). Still, if validated, the *Nasa* system offers promise as a model for investigating plant learning, especially because its stamen movements are relatively fast and unambiguous. This is less laborious than studying learning by waiting for plants to grow slowly toward a stimulus (Gagliano et al., 2016).

8. Downplaying the counterevidence. Although S&C do cite nearly all the opposing literature, they fail to consider the vast majority of the grounds for the concerns raised, and those they do address are dismissed without sufficient reflection. Thus, S&C's analysis is not balanced (Struik, 2023). Objections that should have been considered are:

- a. The electrical signaling in plants travels just one way, with no feedback signals ever having been measured in plant studies. But back-and-forth signaling is needed for the information integration on which sentience depends (Mallatt et al., 2021a, p. 464).
- b. Redefining cognitive terms can lead to confusion and circular reasoning (Taiz et al., 2020; Mallatt et al., 2021c).
- c. The large differences in electrical signaling between animals and plants are downplayed.

Our own publications have documented these electrical differences in depth, starting with the action potentials being fast and started by Na^+ influx in neurons, but slow and started by Ca^{+2} influx in plants (Mallatt et al., 2021a). Therefore, the following statement of S&C (p. 16) sounds self-contradictory to us: "[A]side from the obvious differences between the nervous systems

of animals and the vascular systems of plants, plants lack none of the functional structures that are supposedly needed to be sentient”.

S&C mischaracterize our arguments against plant sentience (p. 18). They say that we view plant behavior as “hardwired,” a term they associate with being “inflexible” and “fixed” (pp. 1, 4), echoing the word “automata” that was wrongly used by Baluska & Mancuso (2021) to describe our conception of plants. We emphatically do *not* consider plant behavior to be either inflexible or fixed, and we never said it was hardwired. We recognize that plants are highly sensitive organisms with many different senses (Mancuso & Viola, 2015) and that they can respond with a large amount of physiological plasticity (Mallatt et al., 2021b).

S&C also quote one of our past statements (p. 18): “Instead of subjective consciousness, plants evolved adaptive behavior that is genetically determined by natural selection and epigenetically determined by environmental factors” (Taiz et al., 2020). S&C apparently take this to mean that we are strict genetic determinists. This is not the case. Our statement includes epigenetics (although epigenetic mechanisms, like all biological capacities, including learning, language and sentience, are of course made possible by genes). By definition, epigenetic modifications give genes new functions that add to plants’ preexisting capacity for flexible homeostatic adjustments to their physiological and behavioral processes. This is the current prevailing view of how plants achieve behavioral flexibility in the absence of sentience.

9. Conclusion. We are heartened by S&C’s shift toward evidence-based and experimental science, but we encourage them to go on to resolve the remaining conceptual problems with plant sentience by correcting the false dichotomy, assuming the burden of proof for extraordinary claims, adopting more parsimonious explanations, divorcing plant sentience from biopsychism, resisting the use of redefined cognitive terms, and taking into account the opposing evidence. The road from romance cannot reach science while denying the burden of proof.

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